

## Dental Eruption Sequence Among Colobine Primates

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**ABSTRACT** Dental development is one aspect of growth that is linked to diet and to life history but has not been investigated among colobines since the work of Schultz [1935]. This study establishes the dental eruption sequence for several colobine species and compares it to that of other catarrhines. The mandibles and maxillae of two hundred and four juvenile colobine specimens were scored for presence or absence of permanent teeth and for stages of partial eruption. Eruption was defined as ranging between tooth emergence (any part of a tooth crown above the alveolar margin) and full occlusion, with three intermediate levels manifest between these boundaries. In African colobines, represented by *C. guereza*, *C. angolensis* and *P. badius*, M2 erupts before I2, and in *C. angolensis* it also erupts before I1. The canine is delayed, erupting after the premolars in females and after M3 in males. Asian colobines show greater diversity in eruption sequences. *Nasalis* shows no early eruption of the molars and is very similar to *Macaca*. In *Trachypithecus* and *Pygathrix* M<sup>2</sup> erupts before I<sup>2</sup>. The canine in *Trachypithecus* is delayed, erupting after the premolars and, in some males, after M3. In *Presbytis* M2 erupts before both incisors; M3 erupts before C in both sexes, and often before both premolars. Although the actual timing of eruption is unknown, all colobine species examined except *N. larvatus* showed some degree of relatively early eruption of M2 and M3. The lack of this tendency in *Nasalis* sets this genus apart from all other colobines represented in this study. Dental eruption sequence is thought to reflect life history patterns. Early molar eruption in colobines was thought by Schultz (1935) to be a primitive character reflecting shorter life history. Faster growth rates found in folivorous primates have been interpreted as being related to an adaptation to folivory (Leigh 1994), and early eruption of molars may be part of this dietary specialization. The relationships between dental development and both diet and life history are investigated. *Am J Phys Anthropol* 112:69–85, 2000.

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The dental development of colobine primates has not been investigated since the work of Schultz (1935) and is largely unknown, as are many other aspects of their growth and life history. Dental development and eruption sequences are considered important indicators of life history patterns, and their study can shed light on the evolution of life history in humans and other primates (Smith 1994). This paper aims to establish the dental eruption sequences in

several colobine genera and to compare them with that of other catarrhines.

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In his seminal study, Schultz (1935) examined material of *Colobus*, *Nasalis*, and *Pygathrix* following the taxonomy of Elliot (1913). Since he did not specify which species he studied, it is not clear to which of the taxa he examined the results of this study correspond. Thus the "*Colobus*" of Schultz (1935) could have included specimens of both *Colobus* and *Procolobus* as used here, while his "*Pygathrix*" might have included *Trachypithecus*, *Presbytis*, and *Semnopithecus* as used here. Schultz (1935) concluded that all three of his colobine genera exhibited a common tendency for early eruption of the second molar. This tendency was less pronounced in *Nasalis* and more pronounced in *Pygathrix*, which also showed very early eruption of the third molar. Schultz (1935) believed that dental eruption sequences reflect overall growth rates and considered that the colobine tendency for relatively early molar eruption indicated a more primitive dental eruption schedule, and hence a shorter growth period and faster growth rates, compared to other catarrhines.

More recently, it has been suggested that dental eruption sequences are indeed very tightly correlated with growth and life history among mammals, but that they do not necessarily indicate phylogenetic relationships (Smith, 1994). Furthermore, the dietary specializations of colobines and other folivorous primates have been implicated in faster growth rates (since folivorous species were found to grow faster in body weight than frugivorous primates of similar body size; Leigh, 1994). Such dietary specializations have also been associated with smaller relative brain sizes in colobines (Clutton-Brock and Harvey, 1980). These findings seem to indicate that colobines have a shorter life history than other catarrhines. However, very little is known about life history variables such as age at menarche and lifespan in colobines, and virtually no ages of dental eruption are known. It is also not clear whether an accelerated life history is conservative for catarrhines or whether it is part of an adaptation to folivory.

By increasing the number of taxa examined and by following a more up-to-date classification, the present study has been

able to expand on the work of Schultz (1935) and to confirm most of his conclusions. Furthermore, it has clarified the patterns of eruption shown by the different colobine taxa examined and emphasized the variability in dental eruption sequences both within and among species and genera. These eruption sequences are considered in the context of growth patterns, life history variables, and dietary adaptations among colobine primates. The results are compared to those obtained by Schultz (1935).

## MATERIALS AND METHODS

The jaws of 204 juvenile colobine primate specimens from the mammalogy collections of the American Museum of Natural History (AMNH) and the National Museum of Natural History (NMNH) were examined, representing the following genera: *Colobus*, *Procolobus*, *Nasalis*, *Simias*, *Pygathrix*, *Presbytis*, *Trachypithecus*, and *Semnopithecus*. Species were identified by locality of capture following the taxonomy given in Napier (1985) and modified according to the classification of Oates et al. (1994) (although Delson in Oates et al. (1994) recognizes *Simias* as a subgenus of *Nasalis* and *Trachypithecus* as a subgenus of *Semnopithecus*). The stage of dental eruption of each specimen was described, and a system of scoring eruption was developed. Zoo specimens and specimens of uncertain specific assignment were excluded from the analysis. The number of specimens, by sex, for each taxon is shown in Table 1.

### Dental eruption: definition and scoring methods

Past studies of dental development in primates have often relied on longitudinal observations from live animals, either through direct observations (Chase and Cooper, 1969; Long and Cooper, 1968; Phillips-Conroy and Jolly, 1988; Reed, 1967; Smith, 1994) or from radiographs (Anemone et al., 1996; Kuykendall, 1996). Among studies of dental eruption sequences that rely on direct observations of museum specimens there is no consensus as to the method of scoring eruption. In living animals a tooth is considered to have erupted if any part of its crown has pierced the gingiva (Smith,

TABLE 1. Numbers of specimens for each taxon studied

	Females	Males	Unknown sex	Total
<i>Colobus</i>	20	20	5	45
<i>C. guereza</i>	14	13	3	30
<i>C. angolensis</i>	6	7	2	15
<i>Procolobus</i>	17	8	4	29
<i>P. badius</i>	15	8	4	27
<i>P. verus</i>	2			2
<i>Nasalis (larvatus)</i>	4	9		13
<i>Simias (concolor)</i>	3	3		6
<i>Presbytis</i>	28	28	4	60
<i>P. hosei</i>	12	3		15
<i>P. melalophos</i>	7	11	2	20
<i>P. rubicundus</i>	3	4		7
<i>P. potenziani</i>	1	3	2	6
<i>P. frontata</i>	3	4		7
<i>P. comata</i>	2	1		3
<i>Pygathrix</i>	6	3		9
<i>P. nemaus</i>	4	1		5
<i>P. roxellana</i>	2	2		4
<i>Trachypithecus</i>	16	21	1	38
<i>T. cristatus</i>	6	11		17
<i>T. phayrei</i>	5	5		10
<i>T. pileatus</i>	4	3	1	8
<i>T. johnii</i>	1	2		3
<i>Semnopithecus (entellus)</i>	2	2		4

1994). This event is the emergence of the tooth. In skeletal material some workers score a tooth as erupted when its crown has risen above the level of the alveolar margin (Schultz, 1935; Thorington and Vorek, 1976), while others prefer to restrict this term to the stage of full occlusion (Cheverud, 1981). Here a tooth was scored as "emerging" when any part of the crown had risen above the alveolar margin.

It is in many cases unclear whether previous studies of dental eruption sequence have used intermediate stages of eruption. Thorington and Vorek (1976) did not discuss this point; Cheverud (1981), Glassman (1983), and Smith (1994) only scored teeth as unerupted or erupted (present/absent). As is evident from his tables and his comments (Schultz, 1935, pp. 520–522; see also Schultz, 1942, p. 297), Schultz appears to have considered the degrees of eruption of each tooth in determining the eruption sequence. In the present study, teeth showing an intermediate level of eruption (between "emerging" and "full occlusion") were further scored to 1/3, 1/2, and 2/3 of the way to full occlusion. When the two sides showed different stages of eruption, the most advanced condition for each tooth was scored,

following Schultz (1935). These intermediate stages of eruption were used in establishing the eruption sequences.

Precedence in the sequence was determined as follows. One tooth was considered to precede another in the sequence if either: a) one was present and the other absent, or b) both teeth had emerged but there was a difference of at least a half step to full occlusion between the two. A strict criterion of presence or absence for the establishment of an eruption sequence is perhaps preferable, particularly when longitudinal data are available or when the samples for the species studied are large, but in the present study two factors made the use of intermediate stages of eruption necessary: a) the sample of specimens for each genus was small, and b) many of the specimens examined showed several teeth in stages of development intermediate between emergence and occlusion, making it difficult to establish the sequence of eruption by simply assessing presence or absence. Further study of wear facets and food staining, as well as work on live animals or radiographs, will be useful in confirming the results obtained in the present study.

The species were combined to represent genera; different species were considered separately when the sample size allowed. Specimens of both sexes, as well as specimens of unknown sex, were first considered together, and a sequence of eruption was established. Specimens of known sex were then separated, and any differences in the eruption sequence of the two sexes were noted. The eruption sequences are presented as "augmented sequences" (Smith, 1994), indicating variability among specimens of the same taxon. The following conventions were used: The order in which a sequence is presented was the most common. Although Smith (1994) used brackets to indicate sequence polymorphisms that occur at high frequencies, in the present study they indicate any sequence polymorphism. The equal sign (=) between two teeth indicates that the two alternative sequences for a particular position occur an equal number of times. Question marks in the eruption sequences indicate that no data were available for that position. In the discussion of

TABLE 2. A: Eruption sequences established by Schultz for three colobine genera (following the taxonomy of Elliot, 1913)

<i>Colobus</i>	M1	I1	M2	I2	P3	P4	C	M3
	M1	I1	[M2	I2]	P3	P4	[C	M3]
<i>Nasalis</i>	M1	I1	[I2	M2]	[P3	P4]	C	M3
	M1	I1	[I2	M2]	C?	[P3	P4]	M3
<i>Pygathrix</i>	M1	M2	I1	I2	M3	[P4	P3]	C
	M1	M2	I1	I2	M3	[P4	P3]	

B: Eruption sequences for seven colobine taxa (following Oates et al., 1994) as established here

<i>C. guereza</i>	M1	I1	M2	I2	[P3 = P4]	[M3	C]	
	M1	I1	I2	M2	P4	[P3	M3 C]	
<i>C. angolensis</i>	M1	[M2	I1]	[I2	P3 = P4]	C	M3	
	M1	M2	I1	I2	P4	[P3	M3 C]	
<i>Procolobus</i>	M1	[I1	M2]	I2	[P3	P4]	[C	M3]
	M1	[I1	I2	M2]	P4	[P3	C	M3]
<i>Nasalis</i>	M1?	I1?	I2	M2	P3?	P4	C	M3
	M1?	I1?	I2	M2	[P3?	P4	C]	M3
<i>Trachypithecus</i>	M1	I1	M2	I2	[P3?	P4	C]	M3
	M1	I1	[I2	M2]	P4	P3	[C	M3]
<i>Presbytis</i>	M1	M2	I1	I2	[M3	P4	P3	C]
	M1	M2	I1	I2	[M3	P4	P3]	C
<i>Pygathrix</i>	M1	[I1	M2]	I2	P3?	P4	C	M3
	M1	I1	M2	I2	C	P3?	P4	M3

the results, n represents the number of informative specimens for the particular position in the taxon under consideration. Data matrices for these taxa are presented in the Appendix.

## RESULTS

The eruption sequences of the colobine taxa examined are presented in Table 2.

### African colobines (Subtribe Colobina)

**Colobus.** Two species were represented in this genus, *C. guereza* and *C. angolensis*. The sample size was large enough for the two species to be considered separately. The sequences of the two species were slightly different (Table 2). In *C. guereza*, M<sup>2</sup> erupts before I<sup>2</sup> in the only specimen available for this position (Fig. 1B). In the mandible, the I<sub>2</sub> M<sub>2</sub> sequence is the only one present (n = 2).

No specimens show M<sup>2</sup> before I<sup>1</sup> (n = 4) or M<sub>2</sub> before I<sub>1</sub> (n = 3). The sequence of the

premolars is variable in the maxilla, the two informative specimens showing opposite conditions. In the mandibles in all four specimens, P<sub>4</sub> erupts before P<sub>3</sub>. Finally, the position of the third molar is variable both in the upper and lower dentition. In 6 of 9 individuals (67%), M<sup>3</sup> erupts before C/, while M<sub>3</sub> erupts before /C in 4 of 6 individuals (67%). Two specimens (one male and one of unknown sex) out of five show M<sub>3</sub> erupting even before P<sub>3</sub>. When the sexes are separated, it is found that the position of the canine relative to the third molar is still polymorphic for both sexes. However, in females, M3 tends to erupt last in both lower and upper jaws, after the canine (2 of 3 specimens for both jaws). In most males (4 of 5), C/ erupts last, after M<sup>3</sup>, and in all males (n = 2), /C erupts after M<sub>3</sub> (Figs. 2B, 3A).

This pattern could be attributed to sexually dimorphic growth of the canine, even though *C. guereza* is noted for the small degree of sexual dimorphism in canine size and for the large size of the female canines (Delson, 1973; Lucas and Teaford, 1994).

*C. angolensis* exhibits a different pattern. The tendency of M2 to erupt early is more pronounced, and this tooth erupts before I1 in 3 of 4 individuals in the upper jaw, and in both lower jaws informative for this sequence position. Unlike *C. guereza*, M2 erupts before I2 in all specimens in both jaws (n = 6 for the maxilla and n = 4 for the mandible). The position of I<sup>2</sup> relative to the premolars is judged polymorphic because in one male specimen, AMNH 52148, both upper premolars erupted before I<sup>2</sup>. This specimen is the only one in this study to show this unusual sequence, which occurs at low frequencies in chimpanzees, and even less frequently in macaques (Smith, 1994). The sequence between the two premolars is similar to that of *C. guereza*: the two informative specimens show opposite conditions in the maxilla, while in the mandible in all four specimens, P<sub>4</sub>s erupt before P<sub>3</sub>s. The position of the canine relative to the third molar seems to vary by sex, as in *C. guereza*. The only female specimen showing this sequence position, AMNH 52157, shows M3 erupting last in both jaws. No males showed this position in the maxilla; in the mandible,



both male specimens show  $M_3$  erupting before  $I_2$ . This evidence suggests sexually dimorphic growth of the canine. In one male specimen,  $M_3$  erupted before  $P_3$ .

In general, the sequences of the two *Colobus* species are similar, and only seem to differ in the position of  $M_2$ , which appears earlier in *C. angolensis*. It may be, however, that the differences detected between the two species are caused by the relatively small sample sizes available. The sequence established for *C. guereza* is similar to that reported by Schultz (1935) for the genus *Colobus*, but it is not clear which species were represented by the specimens that he examined.

**Procolobus.** This study included the species *Procolobus (Piliocolobus) badius* and *Procolobus (Procolobus) verus*. *P. verus* was represented only by two specimens. Even though these taxa are distinguished at the subgeneric level, they were considered together. The combined sequence for *Procolobus* is highly variable, and remains so even when the *P. verus* specimens are removed. The variability in the sequence therefore does not seem to be due to differences between the two taxa. The following discussion pertains to the combined sample of *Procolobus* (Table 2). As in *C. guereza*, the most common sequence in the mandibular dentition is  $I_2 M_2$  (4 of 6 specimens), but the converse sequence,  $M^2 I^2$ , is the only one present in the maxilla ( $n = 3$ ). Both jaws show a slight tendency for  $M_2$  to erupt before  $I_1$  (1 of 5 specimens in both jaws), a sequence that also occurs in *C. angolensis* at a much higher frequency. The sequence at the  $P_3/P_4$  position is variable:  $P^3$  erupts before  $P^4$  in 2 of 3 specimens, while  $P_4$  erupts before  $P_3$  in 3 of 5 specimens. Among males,

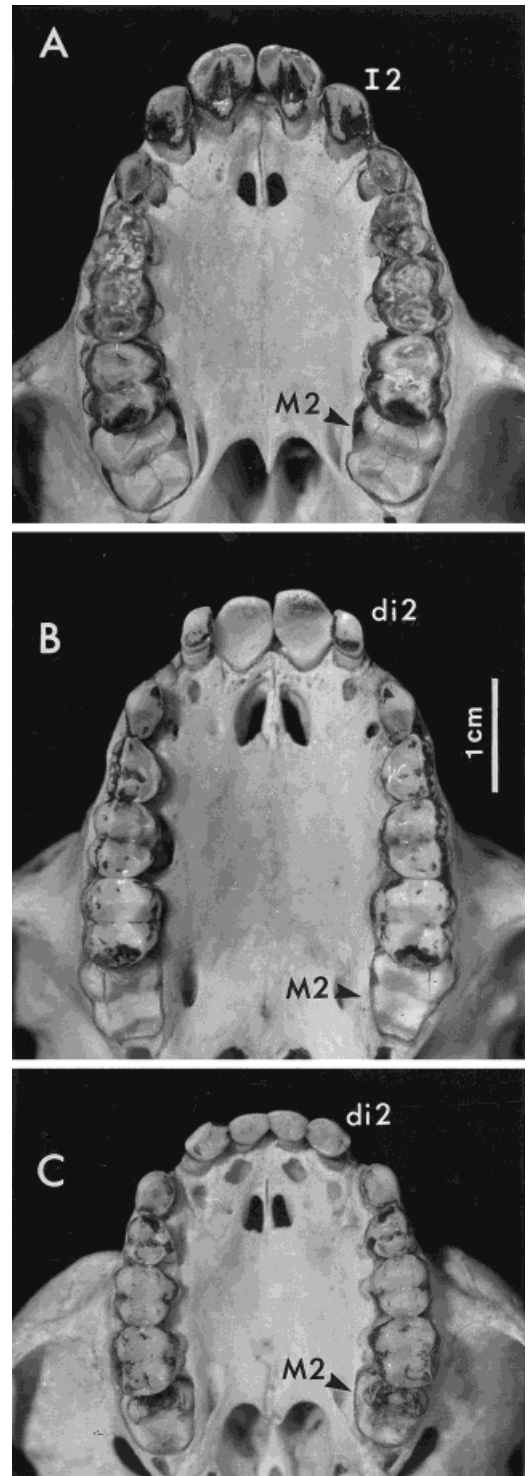


Fig. 1. Stage of eruption of the maxillary permanent incisors relative to the second molar in three colobine species. **A:** *Nasalis larvatus* (AMNH 103463, male), showing both central and lateral permanent incisors in full occlusion and emerging second molar. **B:** *Colobus guereza* (AMNH 81073, female), showing permanent central incisors and deciduous lateral incisors in place and emerging second molar. **C:** *Presbytis frontata* (AMNH 103404, male), showing both central and lateral deciduous incisors in place and emerging second molar.

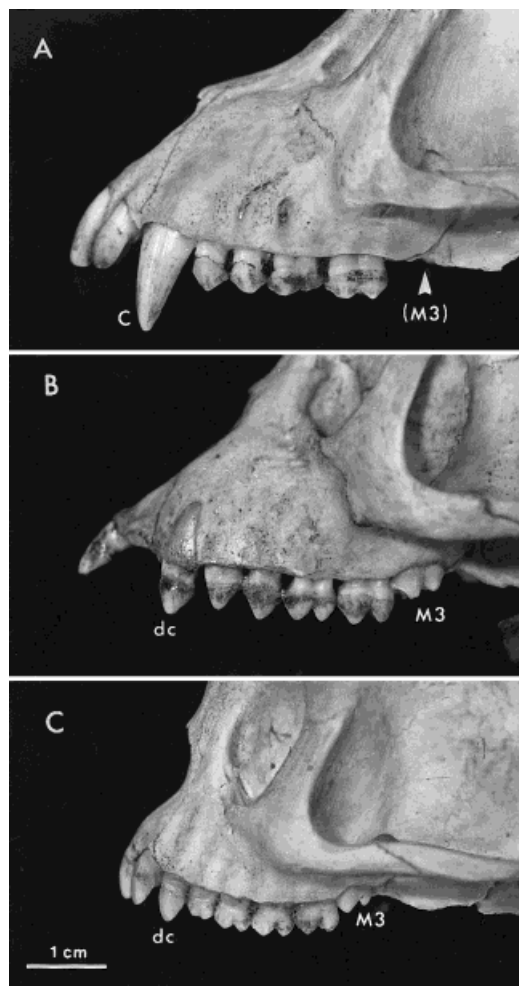


Fig. 2. Stage of eruption of the maxillary permanent canine relative to the third molar in a macaque and in two colobine species. **A:** *Macaca fascicularis* (AMNH 107566, male), showing the permanent canine (C) almost fully occluding and emerging third molar. **B:** *Colobus guereza* (AMNH 52236, female), showing the deciduous canine (dc) in place and the third molar almost halfway to full occlusion. **C:** *Presbytis frontata* (AMNH 103405, female), showing the deciduous canine (dc), as well as the deciduous premolars, in place and emerging third molar.

M<sup>3</sup> erupts before C/ in two specimens each in the maxilla ( $n = 3$ ) and in the mandible ( $n = 4$ ). Females tend to erupt M3 last, with M3 erupting before C in only one specimen both in the maxilla ( $n = 7$ ) and in the mandible ( $n = 4$ ). In two additional specimens of unknown sex, M<sup>3</sup> erupts after C/. In 2 specimens (one male and one female) out of 7, M<sub>3</sub> erupts before P<sub>3</sub>. /C erupts before both

premolars in one female (AMNH 52317), a sequence also observed in female macaques by Smith (1994). In one male (AMNH 52272) /C, as well as both premolars, erupted before M<sub>2</sub>. This is an unusual sequence that does not appear in chimpanzees or pigtail macaques (Smith, 1994).

The remarkable variability observed in this sequence is not due to differences between the two subgenera included, since the sequence is equally variable when *P. badius* is considered alone. However, this high level of sequence polymorphism might possibly be due to differences among the *P. badius* subspecies included (*P. b. temmincki*, *P. b. tephrosceles*, *P. b. oustaletti*, *P. b. tholloni*, *P. b. badius*).

#### Asian colobines (Subtribe Semnopithecina)

**Nasalis.** Thirteen *Nasalis* juveniles were available for study. Based on this small sample size, a tentative sequence was established, which is very similar to that of *Macaca nemestrina* established by Smith (1994) in the positions that could be examined (Table 2). No tendency was observed for M2 to erupt before I2 (Fig. 1A). The two informative specimens for this condition showed fully occluding I2 combined with emerging M2 in both jaws. The only polymorphism found in the *Nasalis* sequence concerns the position of /C relative to the two premolars, and seems to be related to sexual dimorphism. Both males erupted /C after both premolars, while in both females this tooth erupted before both premolars. This polymorphism was also observed in *M. nemestrina*, where in males the canine erupts either between the two premolars, or between P3 and M3, while in females this tooth tends to erupt before the premolars (Smith, 1994). The later eruption of the canine in males suggests a longer growth period for this tooth, which is probably related to the larger size of male canines. M3 was always found to erupt last in both males and females, and in both jaws. In this respect, *Nasalis* again resembles *Macaca* and is unlike several other colobine genera (Fig. 2A). The sequence was not determinable at the M1/I1 and the P3/P4 positions in both jaws.

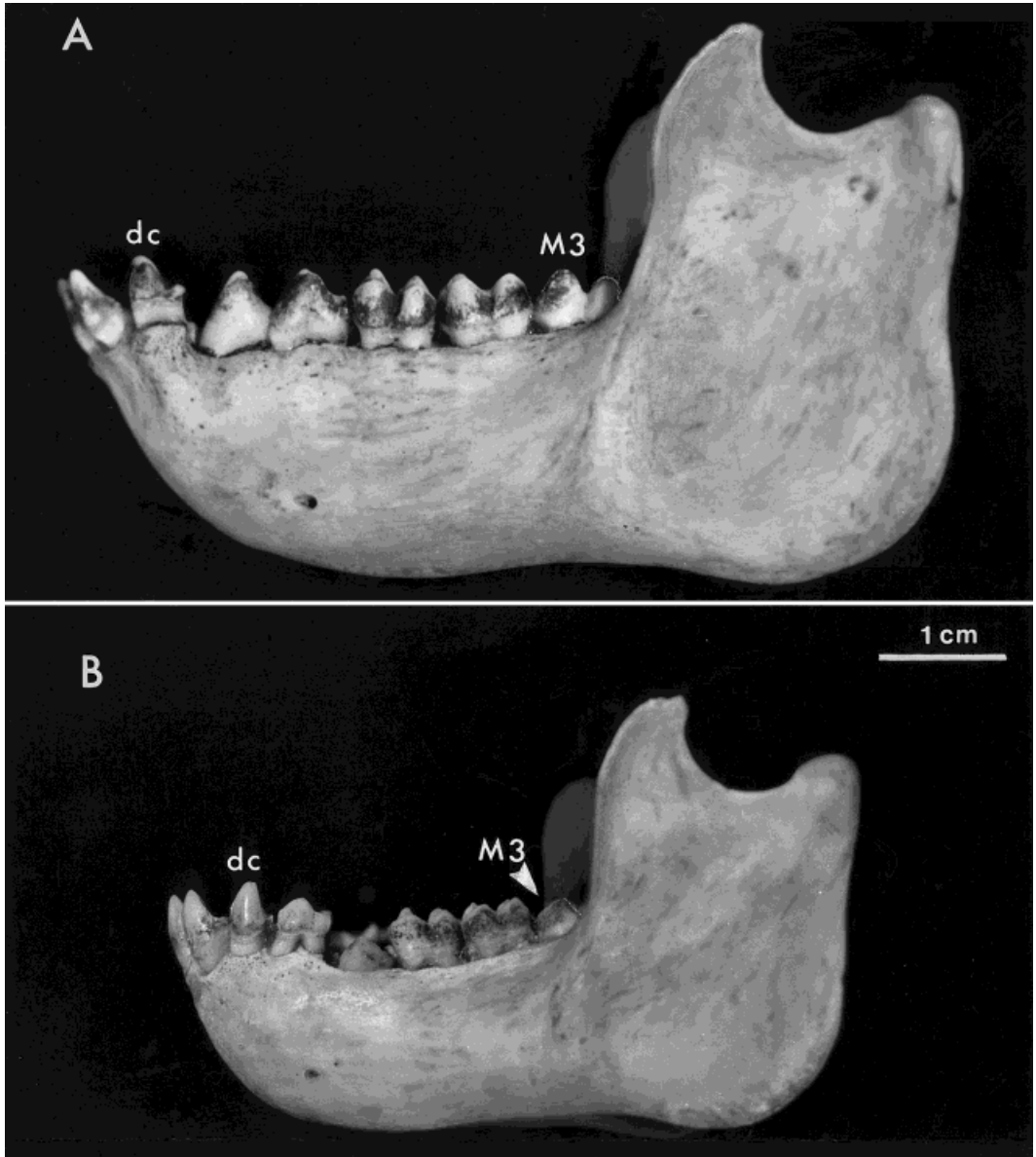


Fig. 3. Stage of eruption of the mandibular permanent canine relative to the third molar in two colobine species. **A:** *Colobus guereza* (AMNH 52236, female), showing the deciduous canine (dc) in place and the third molar almost in full occlusion. **B:** *Presbytis frontata* (AMNH 103405, female), showing the deciduous canine (dc), the deciduous third premolar in place, emerging fourth premolar, and third molar in full occlusion.

Schultz (1935) found the eruption sequence of *Nasalis* to be similar to that of other catarrhines, based on a sample of seven crania. However, he noted a tendency for early eruption of the second molar, which he considered a common characteris-

tic of the three colobine genera that he studied. Such a tendency was not observed in the present study.

***Simias*.** Six specimens of *Simias concolor* were examined. It was not possible to estab-

lish the sequence of eruption, since these individuals did not show most positions of interest. One maxillary and one mandibular specimen showed I1 erupting before M2. In this respect, *Simias* seems different from *Presbytis* or *Colobus angolensis*, but similar to the other taxa examined here. No informative specimens were available for the I2/M2 position or the P3/P4 position. M<sup>3</sup> erupted last in two individuals (one male and one female), as did M<sub>3</sub> in one specimen, a male.

**Trachypithecus.** This genus was represented in this study by the species *T. cristatus*, *T. pileatus*, *T. phayrei*, and *T. johnii*. Among them only *T. pileatus* and *T. cristatus* were represented by large enough samples to be considered separately. No differences were detected between these species; therefore, all *Trachypithecus* specimens were combined. The *Trachypithecus* sequence shows a tendency for early eruption of the second molar, which is more pronounced in the maxilla (Table 2). M<sup>2</sup> always erupts before I<sup>2</sup> (n = 2), while M<sub>2</sub> erupts before I<sub>2</sub> in 1 of 3 specimens. M2 was never observed to erupt before I1 in either jaw. Only one specimen showed the P3/P4 position. In this individual, P<sub>4</sub> erupted first. M3 erupted last in both males and females and in both jaws, with the exception of one male (n = 5), in whom M<sub>3</sub> erupted before /C. In two male maxillae and one mandible, M3 erupted at the same time as C. Finally, in one male specimen (AMNH 113499, n = 6), C/ erupted before both premolars. This sequence polymorphism is common in *M. nemestrina* females, and its presence in a male is unusual. The variability indicated above involving the position of the canine relative to the premolars is due to this specimen.

*Trachypithecus* shares with *C. guereza* a moderate tendency, stronger in the maxilla, for M2 to erupt early, before I2. A weak tendency for early eruption of M3 was also detected. This trend is shared with most of the other taxa examined in this study.

**Presbytis.** This genus was represented by the following species: *P. rubicundus*, *P. melalophos*, *P. potenziani*, *P. frontata*, *P. thomasi*, *P. hosei*, and *P. comata*. Three spe-

cies, *P. melalophos*, *P. hosei*, and *P. frontata*, were represented by large enough samples to be considered separately. All three showed very similar sequences. All specimens were combined and a sequence for the genus was established (Table 2). The M2 I1 sequence, which also appears very frequently in *C. angolensis* and rarely in *Procolobus*, is found in all specimens of *Presbytis* (n = 6 for both jaws). M2 always appears before I2 in both jaws (n = 17 for the maxilla, n = 12 for the mandible) (Fig. 1C). P4 always erupts before P3 (n = 4 in the maxilla, n = 5 in the mandible). M3 emerges extraordinarily early (Figs. 2C, 3B). M3 appears before C in the vast majority of specimens (18 of 19, or 95% in the maxilla, and 13 of 15, or 87%, in the mandible). M3 was found to erupt before C frequently also in *C. guereza*, and less frequently in *C. angolensis* and *Procolobus*. In *Presbytis*, M3 also tends to erupt before one or both premolars in both jaws, but more frequently in the mandible: M3 appears before P3 in 10 of 17 specimens (59%) in the maxilla and in 10 of 13 specimens (77%) in the mandible. M3 erupts before P4 in 9 of 17 specimens (53%) in the maxilla and in 8 of 12 specimens (67%) in the mandible. A tendency for eruption of M3 before P3 is present in the lower jaws of *C. guereza*, *C. angolensis*, and *Procolobus*, where the M<sub>3</sub> P<sub>3</sub> sequence occurs at much lower frequencies (never exceeding 30%) than those presented by *Presbytis*. None of these taxa show this tendency in the upper jaw, nor do they ever show M3 erupting before P4. In this respect, *Presbytis* is unique among the colobine genera studied. The extremely early eruption of M3 could be due to the small size of this tooth, which is reduced in *Presbytis* (Oates et al. 1994).

When the sexes are separated, a dimorphic pattern emerges. In females, M3 tends to erupt before both premolars and the canine, while in males, M3 tends to erupt after the premolars and before the canine. Among females, 8 of 10 specimens show M<sup>3</sup> before P<sup>3</sup>; in 7 of 9 (78%), M<sup>3</sup> erupts even earlier, before P<sup>4</sup>; and 9 of 10 show M<sup>3</sup> erupting before C/. In the mandible, 8 of 9 females (89%) show M<sub>3</sub> before P<sub>3</sub>; 7 of 9 (78%) show M<sub>3</sub> before P<sub>4</sub>; and 9 of 10 show M<sub>3</sub> before /C.



While in most male specimens M3 erupts before the canine (all 9 specimens in the maxilla, and 3 out of 4 in the mandible), M3 erupts before one or both premolars much less frequently than in females: 2 of 7 (29%) show M<sup>3</sup> before P<sup>3</sup> and M<sup>3</sup> before P<sub>4</sub>; only 1 of 3 show M<sub>3</sub> before P<sub>3</sub>, and none (n = 2) show M<sub>3</sub> before P<sub>4</sub>. Here it is not the position of the canine which is sexually dimorphic, since it erupts last in both sexes. It is rather the position of M3 which differs between the sexes, erupting earlier in females. This pattern cannot be explained by longer growth for the male canines, since there is no difference in the relative position of this tooth, unless there are marked differences in the timing of its eruption. However, it must be noted that this pattern may also be due to species-level differences. Most females in whom the third molar erupts before the premolars belonged to *P. hosei*, for which a large number of females was available. There were only three male *P. hosei*, none among them showing this sequence position.

This sequence is very similar to that proposed by Schultz (1935) for his genus *Pygathrix* (sensu Elliot). It is likely that at least some individuals examined in his study actually belonged to *Presbytis* as used here.

**Pygathrix.** The species *Pygathrix* (*Pygathrix*) *nemaeus* and *Pygathrix* (*Rhinopithecus*) *roxellana* were examined. These taxa are distinguished at the subgeneric level, but were pooled here due to the small number of individuals available. The sequence established for this genus (Table 2) shows that M2 erupts before I2 in both the maxilla (n = 3) and the mandible (n = 1). One of 3 individuals also shows M<sup>2</sup> erupting before I<sup>1</sup>, but the one informative specimen for the mandible shows the I1 M2 sequence. The sequence was not determinable at the P3/P4 position. M3 erupts last in both the upper (n = 1) and the lower (n = 2) dentition. /C erupts before both premolars (n = 1, NMNH 258986, a male). This sequence is present in *M. nemestrina* (Smith, 1994) and in *Nasalis*, where it usually appears in females. It is also shown by a single *Trachypithecus* male, AMNH 113499. The only specimen showing the eruption sequence in the maxilla (AMNH 110456) was a female: both premolars

erupted before the canine. It must be noted that the sample size for this genus was very small. The sequence presented here is therefore only tentative.

**Semnopithecus.** Four *Semnopithecus entellus* specimens were examined. They presented no information on the sequence of eruption of the incisors and the second molar, or of the two premolars. In 3 of 4 specimens (2 females and 1 male), M<sup>3</sup> erupted last, while in one male M<sup>3</sup> erupted before C/. In this specimen M<sub>3</sub> also erupted before /C, while in two other individuals (one female and one male), M<sub>3</sub> erupted last.

## DISCUSSION

This study has confirmed the finding of Schultz (1935) that colobines differ from other catarrhines in their dental eruption sequences in that their second and third molars tend to erupt early relative to the other permanent teeth. Most colobine genera studied except *Nasalis* show various degrees of advancement in the relative eruption of the molars: Although Schultz (1935) found that in *Nasalis* the second molars erupted early, no such tendency was observed here. Its eruption sequence as far as can be determined is identical to that of *Macaca nemestrina*. *Presbytis* shows the most extreme expression of the trend for early molar eruption, with the second molar always erupting before both incisors, and the third molar almost always erupting before the canine and very often before one or both premolars in both jaws. *Colobus*, *Procolobus*, *Trachypithecus*, and *Pygathrix* all show intermediate degrees of expression of these tendencies (Figs. 1–3). *C. guereza* and *Trachypithecus* often have the second molar erupting before the second incisor, but never before the first incisor. All other taxa show the M2 I1 sequence at various frequencies, *Procolobus* and *Pygathrix* relatively rarely and *C. angolensis* very frequently. *Trachypithecus* shows a weak tendency for eruption of the third molar before the canine, as does *Semnopithecus*. This tendency is stronger in *Colobus* and *Procolobus*, where the mandibular third molar sometimes erupts even before the third premolar.

Sequence polymorphisms involving the position of the second molar relative to the incisors are rare in macaques and chimpanzees. Smith (1994) found that in male *Macaca nemestrina*, M2 erupts before I2 at a 2% frequency in both maxillary and mandibular dentition, while in females it occurs at a 2% frequency in the mandible and never in the maxilla. In *Pan troglodytes*, an M2 I2 sequence appears at frequencies of 28% in the maxilla and 13% in the mandible. Smith (1994) reported no occurrence of the M2 I1 sequence in macaques, but found an incidence of 3% frequency in the maxilla and 7% frequency in the mandible of chimpanzees. Polymorphisms involving the position of the M3 were not observed among macaques or chimpanzees, where this tooth always appeared last.

#### Dental eruption sequence and life history patterns

The sequence of dental eruption is thought to reflect life history patterns. Schultz (1935, 1960) believed that in "primitive" primates (probably meaning tupaids) the molars were the first permanent teeth to erupt. Only after all the molars had appeared did the permanent incisors, premolars, and canines replace the deciduous dentition. Among "higher" primates, the tendency to prolong the growth period caused the appearance of the molars to be delayed, while replacement of the deciduous teeth occurred earlier in the sequence. As humans have the most prolonged growth period among primates, they were also thought by Schultz (1935, 1960) to be the most "advanced" in their dental eruption sequence, with the second molar erupting only after all the deciduous teeth have been replaced. This scheme implied that, at least among primates, there is a correlation between phylogeny as represented by evolutionary grade, growth prolongation, and relative timing of eruption of the molars. Schultz (1935) believed that the colobine eruption sequence, showing a relatively early eruption of the molars, was primitive for catarrhines. Rather than emphasizing the dichotomy between primitive and advanced, Smith (1994) differentiated between fast-growing and slow-growing mam-

mals and pointed out that eruption sequences probably do not reflect phylogenetic relationships. She agreed with Schultz (1935) that in fast-growing mammals the molars erupt first and then the rest of the permanent dentition appears, while in slow-growing mammals, such as humans, late eruption of the molars relative to the permanent incisors and premolars occurs because they tend to replace the deciduous dentition first and then add the distal molars. This fact is explained, in her view, by the need to maintain functional dentition over a much longer period of growth. If dental eruption sequence reflects life history, the early eruption of the colobine molars probably indicates faster growth rates and shorter life history phases compared to other catarrhines, but it is not necessarily a primitive retention.

It is not clear whether colobines show a general acceleration of life history. Data on ages of dental eruption and on other life history variables, such as age at menarche and lifespan, are known for very few colobine species. Leigh (1994) found that colobines and other folivorous primates tend to grow faster in body weight, and to cease growth relatively earlier, than frugivorous primates of similar size. In her study of *T. cristatus* males, Wolf (1984) found that these animals completed their dental development at an average age of 3.75 years. By comparison, the male *Macaca fascicularis*, a slightly smaller animal (Smith and Jungers, 1997), completes its dental development after 5.5 years, a much later age (Smith et al., 1994). Menarche is known to occur between 25.8 and 29 months of age (Sommer et al., 1992) in free-ranging *Semnopithecus entellus entellus* females, at a body size of about 10 kg (Smith and Jungers, 1997). Wild *Papio hamadryas cynocephalus* females, at a slightly larger body size of about 12 kg (Smith and Jungers, 1997), reach menarche much later, between 48 and 66 months (Altmann and Altmann, 1981). The smaller *Macaca mulatta* females (5.37–8.8 kg, Smith and Jungers, 1997) reach menarche slightly earlier, between 24.1 and 27.8 months, in captivity (Van Wagenen, 1952; Catchpole and Van Wagenen, 1975). It is difficult to determine whether the differences in these

life history variables are as large as would be expected given the differences in body size between the taxa involved, but the limited available evidence suggests that at least some colobines may be characterized by a relatively accelerated life history. Colobines were also found to have a smaller brain size relative to other anthropoids (Clutton-Brock and Harvey, 1980; Harvey et al., 1987; but note that the body mass estimates used by these authors have been questioned by Smith and Jungers, 1997). As brain size tightly correlates with other life history variables, such as body weight, age at weaning, and age at first breeding (Smith, 1989a,b), this finding also points to a relatively accelerated life history.

#### Dental eruption sequence and other variables

The faster growth rates found in some colobine species have been thought by Leigh (1994) to be related to their folivorous dietary adaptation. Folivory has also been implicated in the smaller relative brain size found in the subfamily (Clutton-Brock and Harvey, 1980; Harvey et al., 1987). Colobines are known for their folivorous dietary specializations, and perhaps early molar eruption is part of this adaptation rather than just a side effect of faster growth rates. A folivorous diet may require earlier deployment of molars for processing leaves. Accelerated molar development was found by Dirks (2000) in the folivorous species *Semnopithecus entellus* and *Hylobates syndactylus*, when compared to frugivorous species of the same family in her study of histologically determined chronology of dental development. Folivory was also thought to explain early dental development in leaf-eating lemurs by Godfrey (Seachrist, 1996). However, I have shown that, within colobines, the taxa with earliest molar appearance are not necessarily the most folivorous. *Presbytis*, the genus with the relatively earliest eruption of the molars, is less folivorous than some of the other colobines examined here, such as *Trachypithecus* and *Colobus guereza* (Lucas and Teaford, 1994; Bennett and Davies, 1994), both of which show a much less pronounced tendency for early molar appearance. On the other hand,

*Nasalis*, whose diet comprises fruit, seeds, young leaves, and a very small component of mature leaves (Bennett and Davies, 1994), shows no differences in its dental eruption sequence from a macaque as far as can be determined. Its eruption sequence could be related to its selective feeding habits, or to its large body size.<sup>1</sup>

*Nasalis* is set apart from all the other colobine taxa examined here, both Asian and African, by the lack of any tendency for early eruption of the molars. This finding could also be interpreted as supporting Groves (1989), who suggested that the proboscis monkey is the sister group to all other colobines. In this interpretation the eruption sequence of *Nasalis* and *Macaca* would be primitive for catarrhines, while those of the other colobines would be derived, with *Presbytis* showing the most derived eruption sequence. However, as only a small number of *Nasalis* specimens were available for this study, further work is needed to confirm this result, as well as to determine the usefulness of eruption sequences in phylogenetic analyses (Smith, 1994).

This study found that colobines tend to erupt the fourth premolar before the third. The P4 P3 sequence was the predominant condition in *Colobus*, *Trachypithecus*, and *Presbytis*, and also occurred often in *Procolobus*. Schultz (1935) noted the variability in the P3/P4 position, but found the P4 P3 sequence to be predominant only in *Pygathrix* (sensu Elliot, 1913, including *Trachypithecus*, *Presbytis*, and *Semnopithecus* as used here). The P4 P3 sequence polymorphism was found to occur at high frequencies in both macaques and chimpanzees by Smith (1994), who noted that the two premolars often erupt very close to each other. Therefore, the P4 P3 sequence is by no means unusual in catarrhines. Claims that such a sequence indicates a platyrrhine life history (Simons and Rasmussen, 1996), characterized by short offspring dependency

<sup>1</sup>However, there does not seem to be a direct relationship between early molar eruption and size. Although the smallest colobine, *Presbytis*, shows the earliest placement of the molars, and the largest, *Nasalis*, does not show this tendency at all, *Pygathrix*, also a large colobine, shows early eruption of the second molar.

periods and early sexual maturation, are not substantiated.

Sexual dimorphism in the dental eruption sequence was found in several of the colobine genera studied, and it usually involved the position of the canine. No sexually dimorphic pattern involving the position of the premolars relative to each other was observed. The position of the canine was also found to be dimorphic in macaques. In *M. nemestrina* males, the canine tends to erupt after both premolars, while females show canine eruption before the premolars (Smith, 1994). A similar pattern was observed here in *Nasalis*, suggesting a sexually dimorphic growth trajectory of the canine very similar to that observed in *M. nemestrina*. All other genera studied showed a delay of the canine relative to the premolars in both males and females, with C erupting after P3 and P4. Sexual dimorphism in the eruption sequence involves the position of the canine relative to the third molar. In *C. guereza* males the canine tends to erupt after the third molar, while in females the third molar tends to erupt last. A similar sexually dimorphic pattern is suggested, but could not be convincingly demonstrated, in *C. angolensis*, *Procolobus*, *Trachypithecus*, and *Semnopithecus*. Within the genus *Presbytis*, the third molar tended to erupt in females before one or both of the premolars, as well as before the canine, while in males the third molar tended to erupt before the canine but after the premolars. Here it is the position of the third molar which is sexually dimorphic, erupting earlier in females. This pattern cannot be explained by longer growth for the male canine, since this tooth erupts last in both sexes, but may be related to the reduced size of the third molar in this species.

The subtribe Semnopithecina (Asian colobines) encompasses much greater diversity in dental eruption sequences than does the African subtribe (Colobina), probably reflecting the much greater taxonomic and ecological diversity of the Asian group (Bennett and Davies, 1994; Brandon-Jones, 1984; Oates et al., 1994; Oates, 1994). Sequence variability is also pronounced within the individual colobine taxa examined. In most cases this does not appear to be due to pooling of species into genera for analysis,

but larger samples are needed to resolve this question.

## CONCLUSIONS

This study has shown that at least some colobine genera exhibit a dental eruption sequence that differs from that of other catarrhines, including *Macaca*, *Papio*, and *Pan*, as was previously reported by Schultz (1935). Furthermore, it has demonstrated that there is great variability among colobine genera in this sequence, with differences sometimes appearing at the species level. All colobine genera examined here, except *Nasalis*, showed an early eruption of the second molar, before the second incisor and sometimes before the first incisor. Furthermore, in *Presbytis*, and often *Colobus*, *Procolobus*, and *Trachypithecus*, the third molar also erupted at a very early position, before the canine and sometimes even before the premolars. The sequence of eruption of the two premolars was variable, with the fourth premolar usually erupting before the third. Early molar eruption in colobines is thought to be related to faster growth rates and an accelerated life history (Schultz, 1935; Smith, 1994). Data on life history variables exist only for very few species, but they seem to confirm this hypothesis. They also indicate that colobine primates grow faster than frugivorous primates of similar body size (Leigh, 1994). These findings suggest that faster growth rates may be part of their folivorous adaptation. Folivorous primates are also thought to develop their molars faster than frugivores (Dirks, 2000). Early molar eruption in colobines might also be related to folivory. However, within the subfamily, variation in eruption sequences among different colobine taxa is not consistent with this hypothesis.

The relationships between dental eruption sequence and diet, and between dental eruption sequence and life history, cannot be convincingly demonstrated at present. It appears likely that dental development reflects a compromise between constraints of phylogeny, size, facial architecture, and diet. As always, more data for actual eruption ages, growth, and life history are needed to resolve these questions.



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### APPENDIX

The data were tabulated into pairwise sequences for each taxon and presented in matrices showing the frequency of both al-

ternative sequences for any two teeth (i.e., A before B or B before A). Similar matrices were used by Smith (1994) to illustrate eruption sequence polymorphisms and their frequencies in humans, macaques, and chimpanzees. The sequence shown across the top and down the left side of the matrices is the eruption sequence of *Macaca nemestrina*, as presented in Smith (1994): M1 I1 I2 M2 P3 P4 C M3. This sequence is also present in *M. mulatta*, *M. fuscata*, *Papio hamadryas*, and *Pan troglodytes* (Smith et al., 1994; Smith, 1994), and is thought to characterize many anthropoids (Schultz, 1935). It was used here as a baseline in order to show clearly and in summary the differences between the macaque sequence of dental eruption and that of the colobines examined.

## Appendix

C. guereza Maxilla

	M1	I1	I2	M2	P3	P4	C	M3
M1		10/10	14/14	14/14	18/18	18/18	28/28	26/26
I1	0		5/5	5/5	9/9	9/9	19/19	17/17
I2	0	0		0	5/5	5/5	15/15	12/12
M2	0	0	1/1		6/6	6/6	16/16	14/14
P3	0	0	0	0		1/2	11/11	8/8
P4	0	0	0	0	1/2		10/11	8/8
C	0	0	0	0	0	1/11		3/9
M3	0	0	0	0	0	0	6/9	

C. angolensis

	M1	I1	I2	M2	P3	P4	C	M3
M1		7/7	10/10	6/6	10/10	10/10	14/14	15/15
I1	0		3/3	1/4	3/3	3/3	7/7	8/8
I2	0	0		0	1/1	2/3	6/6	7/7
M2	0	3/4	6/6		6/6	6/6	10/10	11/11
P3	0	0	0	0		1/2	5/5	6/6
P4	0	0	1/3	0	1/2		5/5	6/6
C	0	0	0	0	0	0		1/1
M3	0	0	0	0	0	0	0	

Procolobus

	M1	I1	I2	M2	P3	P4	C	M3
M1		6/6	12/12	11/11	16/16	16/16	22/22	27/27
I1	0		6/6	4/5	10/10	10/10	16/16	21/21
I2	0	0		0	6/6	6/6	12/12	17/17
M2	0	1/5	3/3		8/8	8/8	14/14	19/19
P3	0	0	0	0		2/3	8/8	14/14
P4	0	0	0	0	1/3		7/7	13/13
C	0	0	0	0	0	0		9/12
M3	0	0	0	0	0	0	3/12	

Mandible

	M1	I1	I2	M2	P3	P4	C	M3
M1		9/9	10/10	12/12	23/23	19/19	25/25	24/24
I1	0		1/1	3/3	12/12	9/9	16/16	15/15
I2	0	0		2/2	12/12	10/10	16/16	14/14
M2	0	0	0		11/11	9/9	15/15	14/14
P3	0	0	0	0		0	5/5	4/6
P4	0	0	0	0	4/4		7/7	6/6
C	0	0	0	0	0	0		2/6
M3	0	0	0	0	2/6	0	4/6	

	M1	I1	I2	M2	P3	P4	C	M3
M1		6/6	8/8	4/4	13/13	9/9	14/14	15/15
I1	0		3/3	0	8/8	4/4	9/9	10/10
I2	0	0		0	5/5	1/1	6/6	7/7
M2	0	2/2	4/4		9/9	5/5	10/10	11/11
P3	0	0	0	0		0	3/3	3/4
P4	0	0	0	0	4/4		5/5	6/6
C	0	0	0	0	0	0		1/3
M3	0	0	0	0	1/4	0	2/3	

	M1	I1	I2	M2	P3	P4	C	M3
M1		5/5	8/8	10/10	17/17	17/17	19/19	18/18
I1	0		2/2	4/5	11/11	11/11	13/13	14/14
I2	0	0		4/6	11/11	11/11	13/13	14/14
M2	0	1/5	2/6		10/10	10/10	12/12	13/13
P3	0	0	0	1/11		2/5	4/5	5/7
P4	0	0	0	1/11	3/5		4/5	5/5
C	0	0	0	1/13	1/5	1/5		5/8
M3	0	0	0	0	2/7	0	3/8	

(continued)

Appendix (continued)

Maxilla								
Nasalis								
	M1	I1	I2	M2	P3	P4	C	M3
M1		—	—	2/2	8/8	8/8	10/10	12/12
I1	—		—	2/2	8/8	8/8	10/10	12/12
I2	—	—		2/2	8/8	8/8	10/10	12/12
M2	0	0	0		8/8	8/8	10/10	12/12
P3	0	0	0	0		—	2/2	4/4
P4	0	0	0	0	—		2/2	4/4
C	0	0	0	0	0	0		2/2
M3	0	0	0	0	0	0	0	

Mandible								
	M1	I1	I2	M2	P3	P4	C	M3
M1		—	—	2/2	8/8	8/8	8/8	11/11
I1	—		—	2/2	8/8	8/8	8/8	11/11
I2	—	—		2/2	8/8	8/8	8/8	11/11
M2	0	0	0		8/8	8/8	8/8	11/11
P3	0	0	0	0		—	2/4	3/3
P4	0	0	0	0	—		2/4	3/3
C	0	0	0	0	2/4	2/4		5/5
M3	0	0	0	0	0	0	0	

Simias								
	M1	I1	I2	M2	P3	P4	C	M3
M1		2/2	3/3	3/3	4/4	4/4	4/4	6/6
I1	0		1/1	1/1	2/2	2/2	2/2	4/4
I2	0	0		—	1/1	1/1	1/1	3/3
M2	0	0	—		1/1	1/1	1/1	3/3
P3	0	0	0	0		—	—	2/2
P4	0	0	0	0	—		—	2/2
C	0	0	0	0	—	—		2/2
M3	0	0	0	0	0	0	0	

	M1	I1	I2	M2	P3	P4	C	M3
M1		2/2	3/3	3/3	4/4	4/4	4/4	5/5
I1	0		1/1	1/1	2/2	2/2	2/2	3/3
I2	0	0		—	1/1	1/1	1/1	2/2
M2	0	0	—		1/1	1/1	1/1	2/2
P3	0	0	0	0		—	—	1/1
P4	0	0	0	0	—		—	1/1
C	0	0	0	0	—	—		1/1
M3	0	0	0	0	0	0	0	

Trachypithecus								
	M1	I1	I2	M2	P3	P4	C	M3
M1		10/10	16/16	14/14	28/28	28/28	34/34	38/38
I1	0		7/7	5/5	19/19	19/19	26/26	29/29
I2	0	0		0	14/14	14/14	20/20	24/24
M2	0	0	2/2		15/15	15/15	21/21	25/25
P3	0	0	0	0		—	6/7	9/9
P4	0	0	0	0	—		6/7	10/10
C	0	0	0	0	1/7	1/7		7/7
M3	0	0	0	0	0	0	0	

	M1	I1	I2	M2	P3	P4	C	M3
M1		10/10	13/13	13/13	29/29	28/28	33/33	37/37
I1	0		5/5	4/4	21/21	20/20	25/25	29/29
I2	0	0		2/3	17/17	16/16	21/21	25/25
M2	0	0	1/3		17/17	16/16	21/21	25/25
P3	0	0	0	0		0	6/6	9/9
P4	0	0	0	0	1/1		6/6	10/10
C	0	0	0	0	0	0		6/7
M3	0	0	0	0	0	0	1/7	

(continued)

## Appendix (continued)

## Maxilla

## Presbytis

	M1	I1	I2	M2	P3	P4	C	M3
M1		17/ 17	28/ 28	14/ 14	41/ 41	40/ 40	53/ 53	45/ 45
I1	0		11/ 11	0	24/ 24	23/ 23	36/ 36	26/ 26
I2	0	0		0	16/ 16	15/ 15	28/ 28	20/ 20
M2	0	6/6	17/ 17		30/ 30	29/ 29	42/ 42	34/ 34
P3	0	0	0	0		0	13/ 15	7/ 17
P4	0	0	0	0	4/4		15/ 17	8/ 17
C	0	0	0	0	2/ 15	2/ 17		1/ 19
M3	0	0	0	0	10/ 17	9/ 17	18/ 19	

## Mandible

	M1	I1	I2	M2	P3	P4	C	M3
M1		16/ 16	22/ 22	12/ 12	42/ 42	38/ 38	46/ 46	37/ 37
I1	0		6/6	0	26/ 26	22/ 22	30/ 30	21/ 21
I2	0	0		0	22/ 22	18/ 18	26/ 26	17/ 17
M2	0	6/6	12/ 12		32/ 32	28/ 28	36/ 36	26/ 26
P3	0	0	0	0		0	5/6	3/ 13
P4	0	0	0	0	5/5		9/9	4/ 12
C	0	0	0	0	1/6	0		2/ 15
M3	0	0	0	0	10/ 13	8/ 12	13/ 15	

## Pygathrix

	M1	I1	I2	M2	P3	P4	C	M3
M1		2/2	4/4	3/3	7/7	7/7	8/8	9/9
I1	0		2/2	2/3	5/5	5/5	6/6	7/7
I2	0	0		0	3/3	3/3	4/4	5/5
M2	0	1/3	3/3		6/6	6/6	7/7	8/8
P3	0	0	0	0		—	1/1	2/2
P4	0	0	0	0	—		1/1	2/2
C	0	0	0	0	0	0		1/1
M3	0	0	0	0	0	0	0	

	M1	I1	I2	M2	P3	P4	C	M3
M1		2/2	2/2	2/2	7/7	7/7	7/7	9/9
I1	0		1/1	1/1	6/6	6/6	6/6	8/8
I2	0	0		0	5/5	5/5	5/5	7/7
M2	0	0	1/1		6/6	6/6	6/6	8/8
P3	0	0	0	0		—	0	2/2
P4	0	0	0	0	—		0	2/2
C	0	0	0	0	1/1	1/1		3/3
M3	0	0	0	0	0	0	0	

## Semnopithecus

	M1	I1	I2	M2	P3	P4	C	M3
M1		—	—	—	—	—	1/1	3/3
I1	—		—	—	—	—	1/1	3/3
I2	—	—		—	—	—	1/1	3/3
M2	—	—	—		—	—	1/1	3/3
P3	—	—	—	—		—	1/1	3/3
P4	—	—	—	—	—		1/1	3/3
C	0	0	0	0	0	0		3/4
M3	0	0	0	0	0	0	1/4	

	M1	I1	I2	M2	P3	P4	C	M3
M1		—	—	—	—	—	1/1	2/2
I1	—		—	—	—	—	1/1	2/2
I2	—	—		—	—	—	1/1	2/2
M2	—	—	—		—	—	1/1	2/2
P3	—	—	—	—		—	1/1	2/2
P4	—	—	—	—	—		1/1	2/2
C	0	0	0	0	0	0		2/3
M3	0	0	0	0	0	0	1/3	



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